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Research Article

I eat what my mother eats. Maternal effects on food preferences in invasive amphipods

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Abstract

Invasive alien species achieve their success through a set of traits that give them a fitness advantage over other species. Many of them are characterised by a generalist diet with an inclination to carnivory. The feeding habits of aquatic animals depend on environmental conditions operating at the population level, but the population origin and genetic background are rarely taken into account. Therefore, this study aimed to investigate the effect of the intraspecific genetic variability on the inheritance of feeding habits. We bred individuals of an invasive amphipod, *Dikerogammarus villosus* (Sowinsky, 1894), under semi-natural conditions in a mesocosm system, interbreeding genetically differentiated invasive populations originating from geographically isolated areas (Danube and Dnieper Deltas) or by inbreeding within the populations. We then tested food preferences of the F1 offspring (n = 256) in a 24-hour experiment providing them three food types: leaves, fish tissue and live chironomid larvae. Our results show that, despite similar breeding conditions applied to all experimental groups, populations of different origins varied in their food preferences. It appeared that the level of necrophagy or predation depended on the origin of the maternal population. Interestingly, inter-population hybrids exhibited a higher predation rate compared to pure strains. Our research shows that some traits related to invasiveness are influenced by the maternal effects and are shaped not only by the environment, but also depend on the population origin. To better predict the course and consequences of invasions, we stress the need to study the biology of invasive species using multiple populations.

Key words: Amphipod breeding cultures, biological invasions, feeding habits, hybridization, interbreeding, intraspecific variability, mesocosm experiment, populations

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Introduction

Hybridisation is a widespread phenomenon in both plants and animals (Mallet 2007). The process of interbreeding between individuals from genetically distinct populations or species can occur naturally in contact zones or be the result of human habitat modifications and induced range changes (Murray et al. 2004; Morgan-Richards et al. 2009). This process contributes to the exchange of genetic material between populations or taxa, which can lead to an enhancement of genetic

diversity, facilitate adaptation to novel environments and an introgression may even cause speciation, particularly common amongst plants (Arnold and Martin 2009; Morgan-Richards et al. 2009). For hybridisation to take place, existing pre- and postzygotic barriers should be incomplete or absent (Abbott et al. 2013). Lack of such barriers between populations of the same species enables hybridisation to occur at the intraspecific level (Arnold et al. 1999; Ellstrand and Schierenbeck 2000). Heterosis (hybrid vigour) is one of the advantages of hybridisation leading to their enhanced environmental tolerance and adaptation to novel habitats, so important for successful colonisation of invasive species (Grant and Grant 1992; Wolfe et al. 2007). Although hybridisation can lead to a reduced fitness or outbreeding depression, in most cases, it remains an evolutionary force for speciation and adaptations to new environments (Taylor and Larson 2019). Therefore, it is crucial to understand the mechanism of hybridisation between populations of invasive species, to better predict their future colonisation potential.

In the context of hybridisation, it remains important to understand the inheritance process. Inherited traits can influence key ecological characteristics of animals, including predator avoidance (Keiser and Mondor 2013), food preferences (Tsang et al. 2024) and life history characteristics (Mousseau and Roff 1987). Commonly, these traits are inherited along the maternal line both in plants and animals (Broadhurst 1961; Monty et al. 2009; Rey et al. 2013; Chivers et al. 2015; Alba et al. 2016). Some traits can be passed from females to the offspring not only through nuclear DNA, but additionally with mitochondrial DNA or epigenetically (Camus et al. 2012; Stäubli and Peters 2021). Some of these heritable traits stay important for invasive species (Whitney and Gabler 2008). Admixture and hybridisation between invasive populations can introduce novel genetic combinations shaping invasive potential at a population level (Ellstrand and Schierenbeck 2000). Therefore, it is important to study the process of inheritance of invasive traits at an intraspecific level.

Invasive alien species (IAS) pose a considerable hazard to local and global biodiversity (Pyšek and Richardson 2010; Mačic et al. 2018). They may alter food webs and some of them even modify environments as environmental engineers (David et al. 2017). Invasive species can successfully outcompete native biota due to flexible feeding behaviour and food opportunism compared to usually narrowly-specialised native species (Kostrzewa and Grabowski 2003; Borcherding et al. 2013; Schmitt et al. 2019). Dietary flexibility allows organisms to respond more dynamically to changing environmental conditions and, consequently, colonise new environments (de Carvalho et al. 2019). Then, invasive generalist predators, using a wide variety of food types and connecting several trophic levels, have a particularly profound negative impact on native communities (Crowder and Snyder 2010). Therefore, it is important to characterise feeding behaviour of IAS to predict the further course of their invasions and their effects on the environment (Park 2004).

Generally, feeding habits may depend on locally variable environmental conditions (Snyder and Evans 2006) and genetic variation between populations (Sotka et al. 2003). Feeding habits and predation efficiency of ectotherms are determined by temperature (Parmenter 1980; Woodward et al. 2010; Cuthbert and Briski 2021). The trophic niche and trophic position of invasive fish may change depending on numerous environmental factors that vary along the course of the river, for example, benthic community structure and vegetation (de Carvalho et al. 2019). Moreover, the diet of IAS may vary between environments differing in chemical composition of water and sediments. For instance, Arbačiauskas et

al. (2013) noted higher predatory levels of brackish populations of the invasive amphipod, *Pontogammarus robustoides* when compared to freshwater populations. All these studies highlight the role of the environment in shaping traits important in the invasion process, including feeding habits of animals, neglecting the genetic component, although the environment together with the genotype shapes these traits. Studying invasive potential at the population level allows us to take into consideration local environmental conditions, the population origin and genetic pool (Haubrock et al. 2024; Alves et al. 2025) though such studies are still rare.

A good model species to study inheritance of feeding habits manifested at the population level is the invasive amphipod – *Dikerogammarus villosus*. This species is amongst the 100 worst alien invasive species in Europe (Nentwig et al. 2018). Its successful colonisation can be attributed mainly to considerable voracity, high level of predation and high fecundity, as well as fast growth and early maturation (reviewed in Rewicz et al. (2014)). *Dikerogammarus villosus* is not specialised to any particular feeding mode (Mayer et al. 2008) and displays a broad range of feeding habits – carnivory, herbivory, detritivory and coprophagy (Dick and Platvoet 2000; Platvoet et al. 2009). *Dikerogammarus villosus* is known for preying on various invertebrate larvae, juvenile crustaceans, leeches, fish fry and eggs, as well as early-stage anurans (Rewicz et al. 2014; Taylor and Dunn 2017; Warren et al. 2021). Despite the feeding opportunism of this species, its populations can vary in diet and trophic position depending on local environmental conditions, including the species composition of potential prey (Hellmann et al. 2015). The diet and level of carnivory of individual populations of *D. villosus* seem to change between native and invaded ranges, with lower trophic position being promoted in the colonised area (Copilaș-Ciocianu et al. 2024). In addition, based on morphological analyses of feeding-related traits, it turns out that brackish populations of *D. villosus* tend to be more predatory compared to their freshwater counterparts (Podwysocki et al. 2025a). Differences in preferred food have also been observed between invasive populations of this species coming from geographically isolated and genetically differentiated source populations (Podwysocki et al. 2025c). It turns out that population origin stays important in shaping the invasive potential of this species.

Rewicz et al. (2015b) noted that *D. villosus* colonised European aquatic environments from two geographically separated and genetically differentiated populations – the Danube and the Dnieper Deltas that formed two genetic groups of this species: the Western and the Eastern ones, respectively, keeping their distinctiveness throughout the course of the invasion. The Western Group spread in the western part of the continent through the River Danube and backwards towards the east via the Mittelland Canal, reaching the River Oder. Simultaneously, the Eastern Group spread through the River Dnieper in Central and Eastern Europe and reached the River Vistula in Poland (Bij de Vaate et al. 2002; Bącela et al. 2008; Podwysocki et al. 2024b).

It has been observed that the Western Group is morphologically adapted to be more predatory, while the Eastern Group favours a rather more omnivorous diet (Podwysocki et al. 2025a). These observations were confirmed by the experimental testing of food preference between both groups, demonstrating a higher selectivity for insect larvae exhibited by the Western Group and a more balanced diet of the Eastern Group (Podwysocki et al. 2025c). The traits that affect invasiveness of this species are shaped not only by the environment, but also by the origin of

the population and the gene pool. For instance, Hupało et al. (2018) discovered that both groups differ in the level of heat shock proteins as a consequence of different origins and surrounding environmental conditions. Populations of this species exhibiting different origin and inhabiting different habits also display differences in competition, leading to discrepancies in their dispersal (Podwysocki et al. 2025b). Distinguishing whether the invasive potential of a population is environmentally or genotypically driven can be a significant challenge for understanding the future invasion of amphipods in cases of interbreeding between populations differing in origin and gene pool.

Currently, the Western Group inhabits the River Oder and the Eastern Group is recorded from the River Vistula – both main rivers in Poland, flowing into the Baltic Sea. A small distance separates them from their meeting (i.e. the Bydgoski Canal connecting the Oder and Vistula Rivers). Rewicz et al. (2015a) suggests that both groups can interbreed and hybridise once they meet, which is expected to happen with time. As both groups show numerous metabolic, morphological and behavioural differences, it is to be expected that their offspring will have mixed traits and, through segregation of desired traits, may achieve genotypes that promote higher invasion potential than that of their parents (Facon et al. 2005; Hegarty 2012; Parepa et al. 2014) and pose a higher threat to the environment compared to initial populations (Hovick and Whitney 2014). Therefore, it is very important to first characterise the invasive potential of the initial populations to better understand and predict the effect of inheritance of invasive traits and interbreeding leading to the formation of hybrids in the future perspective.

Therefore, a mesocosm system was used to create the conditions to interbreed between both groups of *D. villosus*, controlling for the effect of the environment and to obtain F1 generation offspring to test how interbreeding shapes the feeding behaviour. If the next generations of the different groups continue to exhibit differences in food preferences despite being grown under uniform conditions in mesocosm culture, we will interpret this as hereditary traits. Thus, our first hypothesis was that feeding habits in amphipods are heritable (Fig. 1). For instance, such a phenomenon has been observed for a marine amphipod – *Ampithoe longimana* (Sotka and Hay 2002). Moreover, interbreeding between the groups may lead to the segregation of desirable traits amongst hybrids and, consequently, their higher invasive potential. Therefore, our second hypothesis was that offspring from mixed parents show higher consumption rates and higher levels of predation than offspring from pure lines. Our third hypothesis was that food preference in amphipods is subject to the maternal effect, as suggested by results on other taxa (e.g. Rey et al. (2013)).

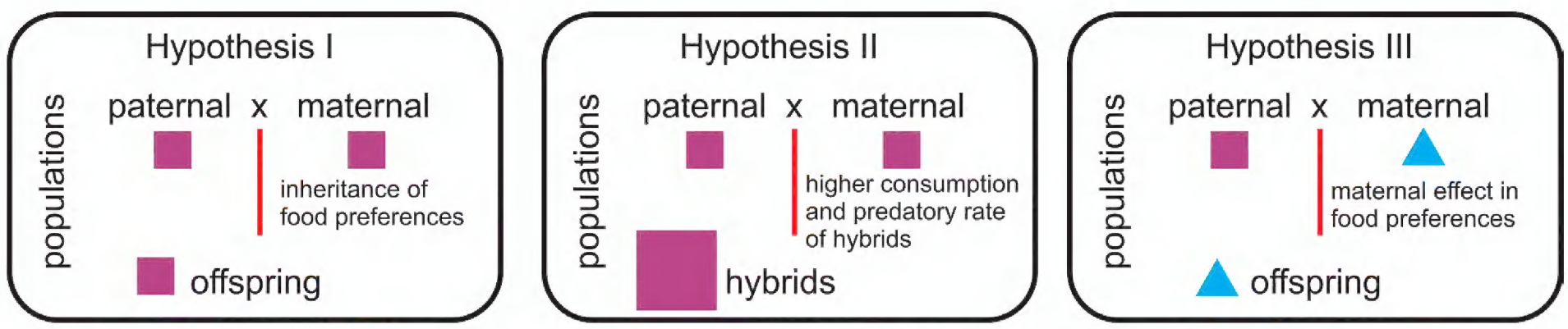

Figure 1. Schematic overview of the work assumptions (the geometric figures represent preferred food types, where the magenta squares represent a specific food category, for example, invertebrate larvae and the cyan triangles represent another food category, for example, fish muscle tissue).

Materials and methods

Sampling

To test for the hereditary differences between two invasive genetic groups of *Dikerogammarus villosus* and their crossbred offspring, we collected live amphipods from two main rivers in Poland: the River Oder (inhabited by the Western Group) and the River Vistula (inhabited by the Eastern Group). To reduce the potential local effect of the site, at each river, we chose two sampling points – the same as in Podwysocki et al. (2025c), i.e. Brzeg (50°52'30.994"N, 17°27'17.465"E) and Zdzieszowice (50°24'42.12"N, 18°6'25.559"E) on the River Oder and Wyszogród (52°23'4.56"N, 20°11'31.2"E) and Ciechocinek (52°52'52.68"N, 18°50'0.6"E) on the River Vistula. We collected animals on 11–12/04/2022 (Fig. 2) by kick-sampling and sweep sampling with a benthic hand-net (1 mm mesh size) from stones and gravel around groynes, following Jażdżewski et al. (2002) and Correa-Araneda et al. (2021). We implemented a modified biosecurity protocol used by U.S. Fish and Wildlife Service (2018) to avoid biocontamination i.e. visual inspection, rinsing with river and distilled water and air-drying all the equipment having contact with river water (e.g. waders, nets, trays, probes). From each site, we collected 800 medium-sized specimens (10–15 mm) without visible signs of injuries or parasites. At the same time, we measured basic water parameters: temperature, pH, conductivity and dissolved oxygen concentration (see Suppl. material 1: table S1). Animals were transported to the mesocosm system (located in shaded area near Lodz on private property of one of the co-authors) in 3.5 litre buckets (200 individuals per bucket, ~ 0.3 l of river water, decomposing leaves on the bottom) placed in styrofoam boxes with ice coolers.

Mesocosm breeding culture

One common method to study invasion biology is breeding invasive species under laboratory or semi-natural conditions. Under laboratory conditions, it is possible to easily carry out cultures and observe aspects of the biology of invasive species (Hyne et al. 2005; Pöckl 2007; Alther et al. 2023). On the other hand, such cultures lack realism resulting from the complexity of natural processes in the environment (Dodd JR 2009). A good alternative to laboratories, where we can still easily control external factors, but provide much more natural conditions, is a mesocosm system. Such systems imitate semi-natural conditions and constitute a platform between easy to conduct, but far from being realistic laboratory studies and reliable although expensive and time-consuming field surveys (James and Boone 2005; Stewart et al. 2013). In the case of amphipods, mesocosm systems served in the experimental testing of species co-existence, competition, temperature preference, migrations and food preference (Duffy and Hay 2000; Cothran et al. 2015; Hellmann et al. 2017; Vander Vorste et al. 2017; Worischka et al. 2018).

In the mesocosm breeding culture, the specimens were divided per sex under a stereomicroscope according to the sex-dimorphism features i.e. more robust gnathopods and dense brush-like bunches of setae in antennae in males (Zettler and Zettler 2017). Then, animals were moved to separate opaque tanks (each sex and sampling site separately) filled with aerated water from a local pond for four weeks of quarantine. The aim of this quarantine was to eliminate

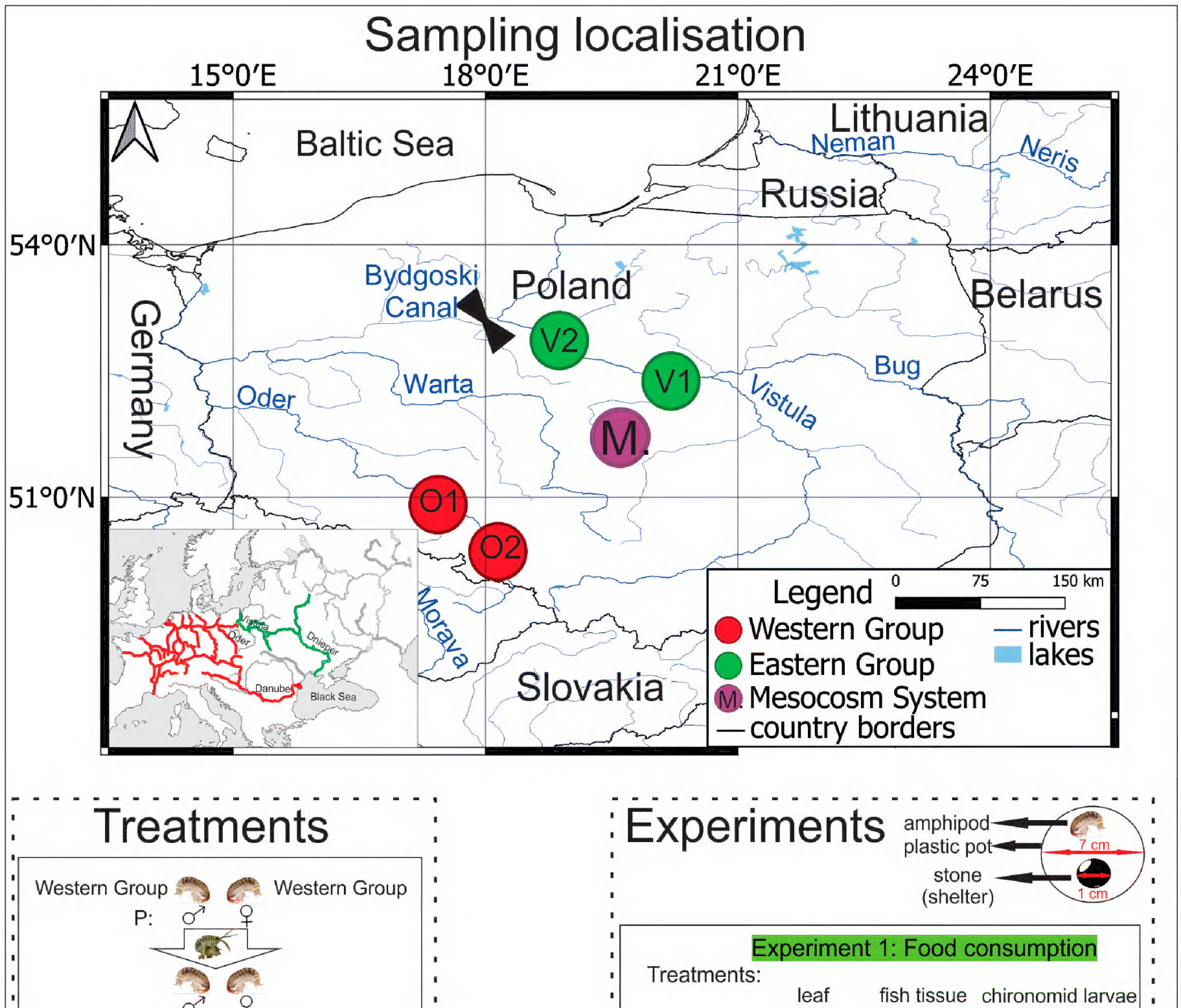

Figure 2. Study area, mesocosm culture and experimental design. Sampling points on the map are numbered as follows: O1 – Brzeg, O2 – Zdzieszowice, V1 – Wyszogród, V2 – Ciechocinek. The map was prepared in QGIS 3.10.13 (QGIS Development Team 2020).

weak, damaged and infected individuals that could obstruct breeding, as well as to give gravid females time to release eggs so that cross-breeding could take place. After a month of quarantine, we again determined the sex of the individuals (double-checking) and counted the surviving individuals (quarantine survival rate was ~ 80%). The specimens were then randomly divided equally amongst four treatments: pure Western Group, pure Eastern Group, Hybrid I (males from the Western Group, females from the Eastern Group), Hybrid II (males from the Eastern Group, females from the Western Group) and put in two cages lined with 1 mm mesh size net and submerged in each of the twelve mesocosm tanks (three tanks per treatment). Amphipods were fed weekly with chironomid larvae and decomposing leaves from the local pond. In addition, the animals had a constant supply of fresh water from the surrounding pond via a pump system. The physicochemical parameters of the water were monitored throughout the culture period (Suppl. material 1: table S1). By carrying out regular observations, we identified the point at which the individuals of the F1 generation, swimming in the tanks, but outside the cages (those at juvenile stage that went through the mesh in the net lining the cages), had reached adult size. F1 specimens were collected from the tanks, separated by sex and transported to the laboratory for the experiments. Cases of cannibalism were observed very rarely and deemed irrelevant.

Pre-experiment procedures

The experimental setup followed the protocol by Podwysocki et al. (2025c). In the laboratory, amphipods from all tanks of one strain were kept together – regular checking of conditions in the tanks allowed us to mix individuals from different tanks. Acclimatisation (24 h) and standardisation of the hunger level (24-h starvation) were implemented in the experimental laboratory at temperature 19 °C ± 1 °C under 10:14 day:night photoperiod (i.e. a total of 48 h at the experimental photoperiod). A longer dark period compared to that commonly used in similar experiments (i.e. 12 h) was used to enhance amphipod activity and emphasise differences between treatments (Czarnecka et al. 2022). For the starvation, each specimen was isolated in a 60 ml vial closed by a 1 mm mesh size net to avoid cannibalism and migration of any food particles and to allow oxygenation at the same time. Vials were placed horizontally in the tanks filled with aerated water. One drop-like black glass stone of diameter 1 cm was put into each vial to serve as a shelter and reduce the level of stress (Jermacz and Kobak 2017). Directly after the starvation period, the animals were used in the experiments.

Experiment I: Food consumption

Due to technical limitations, the experiment was divided into two consecutive days. Circular transparent plastic pots (7 cm in diameter, 4 cm in height) were filled with 60 ml of conditioned laboratory water and randomly assigned to one of the three treatments (food types): decomposing leaves of *Salix alba*, a piece of fish muscle tissue (*Cyprinus carpio*) and live chironomid larvae to test for shredding/grazing, scavenging and predation feeding habits. For several weeks before starting the experiment, willow leaves (terrestrial) were collected and immersed in oxygenated and conditioned tap water to induce the formation of a biofilm

(Medeiros et al. 2009). The frozen fish tissue was defrosted in the laboratory 12 h before the experiment, while chironomid larvae were kept in a tank with water in the fridge (+4 °C).

The food was dried on the filter paper for 5 seconds, weighed with a balance with an accuracy of up to 0.001 g and put into each pot right before the experiment. Each day, four replicates of each food treatment were used i.e. eight in total for the experiment. The mean weight of food in the treatments was: 0.025 g (SD = 0.029 g) for leaf; 0.088 g (SD = 0.034 g) for fish tissue; 0.032 g (SD = 0.007 g) for live chironomid larvae (see Suppl. material 1: table S2). To take into account the possible loss of food weight other than consumption by the amphipods, four control replicates for each food treatment were conducted each day (eight in total). The mean weight of food in the control treatments was: 0.033 g (SD = 0.012 g) for leaf; 0.125 g (0.068 g) for fish tissue; 0.030 g (SD = 0.003 g) for chironomid larvae (see Suppl. material 1: table S3). The differences in the weight of the different types of food were due to the difficulty of measuring similar weights. For this purpose, food was prepared in the following way: leaf fragments of 1 cm^2, fish tissue – cubes of 1 cm^3 and eight chironomid larvae of similar size. Differences in weight between the different types of food were taken into account in the statistical analyses.

Then, individual amphipods with an equal representation of both sexes (previously separated) from each of the four mesocosm strains were randomly placed in the pots with the same stone shelters from the prior starvation period. The experiment was conducted under the same photoperiod as that used during the acclimatisation (i.e. 10:14 h day:night). Each day (2 in total), a total of 24 treatments (two sexes × three food types × four mesocosm treatments), each replicated four times, were conducted, resulting in a total of 192 individuals being tested each time. After 24 h, the remaining food was weighed as described previously. Amphipods were preserved in ethanol (96%) and weighed afterwards. Dead specimens or those that moulted during the experiment, were excluded from further analyses (see Suppl. material 1: table S2).

Experiment II: Food preference

Together with Experiment I, four replicates of the food preference experiment were processed each day. The procedure was identical as in Experiment I with one difference – a mixture of the three food items (i.e. all of them together) was provided to each specimen (mean weights: 0.024 g (SD = 0.011 g) of leaf, 0.083 g (SD = 0.031 g) of dead fish tissue and 0.032 g (SD = 0.005 g) of live chironomid larvae). Each day (two in total), a total of eight treatments (two sexes × four mesocosm treatments), each replicated four times, were conducted (see Suppl. material 1: table S2). In total, 64 specimens were tested. The mean weight of food in the control treatments was: 0.026 g (SD = 0.021 g) for leaf; 0.115 g (SD = 0.093 g) for fish tissue; 0.033 g (SD = 0.009 g) for chironomid larvae (see Suppl. material 1: table S3).

Statistical analysis

Food consumption (Experiment I) and Food preference (Experiment II) were tested with Generalised Linear Mixed Models (GLMMs) using R software 4.3.0 (R Core Team 2023).

Food consumption (Experiment I)

Food consumption was tested separately for each food type. The response variable was obtained from the following formula:

$$food\ consumption\ (g) = (Q1 - Q2) * (C2/C1)$$

where (*Q*) is the amount of food (*g*) before (*1*) and after (*2*) the experiment; (*C*) is the mean amount of food (*g*) in control treatment before (*1*) and after (*2*) the experiment.

The response variable was modelled in a GLMM with Tweedie distribution due to the presence of zero consumption values for some individuals. The basic model contained the full set of interactions between all fixed explanatory variables (origin of the maternal group – Western or Eastern, genotype – pure or hybrid, sex, log-transformed amphipod weight). Sex was used to control for the possible bias associated with different food consumption by males and females. The day of the experiment and tank was used as a random effect. Extreme outliers were omitted from the analyses after visual inspection (a priori exclusion). Next, based on AICc (Akaike Information Criterion with a correction for small sample sizes) (Akaike 1974), we compared the models by reducing random effects and then by reducing step-by-step the particular interactions (see Suppl. material 1: tables S4–S6). Final models (Table 1) were validated by simulating their residuals using the package *DHARMa* (Hartig 2022) (see Suppl. material 1: figs S1–S3). The Wald chi-square test was computed for every model through analysis of deviance with the *Anova* function in the "car" package (Fox and Weisberg 2019). Pairwise comparisons were generated with the emmeans function and Bonferroni adjustments via the "emmeans" package (Lenth 2022). GLMM marginal effects were predicted using the sjPlot package.

Food preference (Experiment II)

The Ivlev's Selectivity Index (Ivlev 1955; Lechowicz 1982) was calculated to assess preferences towards particular food types, while taking into account differences in the amount of food available (it was technically difficult to serve exactly the same volume of each of the three food types to each animal). The index (E_i) was calculated separately for each food item from the formula below:

$$E_i = (r_i - p_i)/(r_i + p_i)$$

where r_i and p_i are the proportions of a given food type i consumed and available at the beginning of the experiment, respectively.

The weight of food consumed was corrected for differences in control treatments before calculating the proportion (r_i).

Food preference was modelled separately for each food item with the Gaussian distribution due to presence of the values between –1 and 1. The basic model contained the interaction between the origin of the maternal group – Western or Eastern; genotype – pure or hybrids; sex and log-transformed amphipod weight. Similar to Experiment I, the day of the experiment was used as random effects. Then, based on AICc, we compared the models by reducing random effect

Table 1. Full models used in the analyses. Interactions between the variables were marked with an asterisk (*). Variables added to the model without interaction were marked with a plus sign (+). (1|variable) means random intercepts. In the column: Factors and levels, factor names are in **bold** with the number of levels in the brackets.

Analysis	Response variable	Full model	Factors and levels
Experiment I: Food consumption	leaf consumption	origin * genotype * sex *amphipod weight (log) + (1|day) + (1|tank), tweedie (link = "log")	**origin** (2): Western, Eastern**; genotype** (2): pure, hybrids; **sex** (2): males, females; **day** (2): 1, 2; **tank** (3): 1, 2, 3
	fish consumption		
	chironomid larvae consumption		
Experiment II: Food preference	selectivity towards leaf	origin * genotype * sex *amphipod weight (log) + (1|day) + (1|tank), gaussian (link = "identity")	**origin** (2): Western, Eastern**; genotype** (2): pure, hybrids; **sex** (2): males, females; **day** (2): 1, 2; **tank** (3): 1, 2, 3
	selectivity towards fish		
	selectivity towards chironomid larvae		

and then reducing step by step the particular interactions (see Suppl. material 1: tables S7–S9). Final models (Table 1) were validated and pairwise comparisons were generated similarly to the analyses in Experiment I, as well as GLMM marginal effects which were predicted (see Suppl. material 1: figs S4–S6).

Results

Leaf consumption

Leaf consumption in Experiment I (mean: 0.01 g/individual/24h; n = 60) significantly differed between the genotypes and amphipods of different weight in the genotype * amphipod weight interaction ($p < 0.01$; Table 2, Fig. 3A). Leaf consumption decreased with an increase in amphipod weight and, amongst larger specimens, it was higher in those of pure genotype compared to hybrids ($p < 0.05$; for pairwise comparisons, see Suppl. material 1: table S10). Leaf consumption was marginally higher in amphipods of Western origin of maternal line (hybrids II) compared to offspring of Eastern origin of maternal line (hybrids I; $p = 0.09$), regardless of whether the genotype was mixed or pure (Table 2, Fig. 4). Fixed effects explained 0.020 (Marginal R^2) of the variance observed.

Fish consumption

Similar to leaf consumption, fish consumption (mean: 0.01 g/individual/24h; n = 55) tended to decrease with an increase in amphipod weight which was genotype-specific ($p = 0.04$; Table 2, Fig. 3B; for pairwise comparisons, see Suppl. material 1: table S11) and was lower in hybrids compared to pure genotype amphipods. Fish consumption was the lowest amongst all food types consumed by amphipods of the Western origin (Fig. 4). The day of the experiment had a significant contribution to the variability observed (Marginal R^2/ Conditional R^2: 0.092/0.364).

Chironomid larvae consumption

Chironomid larvae were the most consumed food item (mean: 0.02 g/individual/24h; n = 59) and it was marginally significantly higher ($p = 0.07$) amongst hybrids compared to pure strains (Table 2, Fig. 4). Fixed effects explained 0.020 (Marginal R^2) of the variance observed.

Table 2. Results of GLMM models for food consumption (results of Experiment I) and food preference (results of Experiment II). An asterisk (*) indicates interaction. Variables added to the model without interaction were marked with a plus sign (+). (1|variable) means random intercept. Significant effects ($p \leq 0.05$) are in **bold**. Marginally significant effects ($0.05 < p < 0.1$) are in *Italics*. Chisq: the chi-square statistic; Df: the degrees of freedom; Pr: p-value.

Model	Response variable	Final model	Factor	GLMM		
				Chisq	Df	Pr (> Chisq)
Experiment I: Food consumption	leaf consumption	origin * genotype * sex * amphipod weight (log), tweedie (link = "log")	*origin*	*2.87*	*1*	*0.09*
			genotype	0.04	1	0.85
			sex	2.67	1	0.10
			amphipod weight (log)	0.03	1	0.87
			genotype * sex	2.45	1	0.12
			genotype * amphipod weight (log)	**8.11**	**1**	**< 0.01**
			sex * amphipod weight (log)	0.81	1	0.37
			genotype * sex * amphipod weight (log)	1.47	1	0.23
	fish consumption	origin * amphipod weight (log) + genotype * amphipod weight (log) + sex * amphipod weight (log) + (1|day), tweedie (link = "log")	origin	0.57	1	0.45
			amphipod weight (log)	0.00	1	0.97
			genotype	0.01	1	0.91
			sex	1.30	1	0.26
			origin * amphipod weight (log)	0.11	1	0.74
			genotype * amphipod weight (log)	**4.23**	**1**	**0.04**
			sex * amphipod weight (log)	0.05	1	0.82
	chironomid larvae consumption	origin * amphipod weight (log) + genotype * amphipod weight (log) + sex * amphipod weight (log), tweedie (link = "log")	origin	0.05	1	0.83
			genotype	*3.20*	*1*	*0.07*
			sex	0.04	1	0.84
			amphipod weight (log)	2.06	1	0.15
			origin* amphipod weight (log)	0.03	1	0.85
			genotype * amphipod weight (log)	0.23	1	0.63
			sex * amphipod weight (log)	1.28	1	0.26
Experiment II: Food preference	selectivity towards leaf	origin + genotype * sex * amphipod weight (log), gaussian (link = "identity")	origin	0.51	1	0.48
			genotype	0.01	1	0.94
			sex	0.46	1	0.50
			amphipod weight (log)	0.01	1	0.94
			*genotype * sex*	*2.82*	*1*	*0.09*
			genotype * amphipod weight (log)	2.39	1	0.12
			sex * amphipod weight (log)	**5.56**	**1**	**0.02**
			*origin * sex * amphipod weight (log)*	*2.91*	*1*	*0.09*
	selectivity towards fish	origin * genotype * amphipod weight (log) + sex * amphipod weight (log), gaussian (link = "identity")	**origin**	**5.75**	**1**	**0.02**
			genotype	0.76	1	0.38
			amphipod weight (log)	**8.26**	**1**	**< 0.01**
			sex	0.12	1	0.73
			*origin * genotype*	*3.00*	*1*	*0.08*
			origin * amphipod weight (log)	0.00	1	0.97
			genotype * amphipod weight (log)	1.51	1	0.22
			sex * amphipod weight (log)	0.63	1	0.43
			origin * genotype * amphipod weight (log)	**4.21**	**1**	**0.04**
	selectivity towards chironomid larvae	origin * amphipod weight (log)+ genotype * amphipod weight (log) + sex * amphipod weight (log), gaussian (link = "identity")	**origin**	**6.48**	**1**	**0.01**
			genotype	0.59	1	0.44
			amphipod weight (log)	0.70	1	0.40
			sex	0.23	1	0.63
			origin * amphipod weight (log)	0.01	1	0.94
			genotype * amphipod weight (log)	**4.49**	**1**	**0.03**
			sex * amphipod weight (log)	0.97	1	0.32

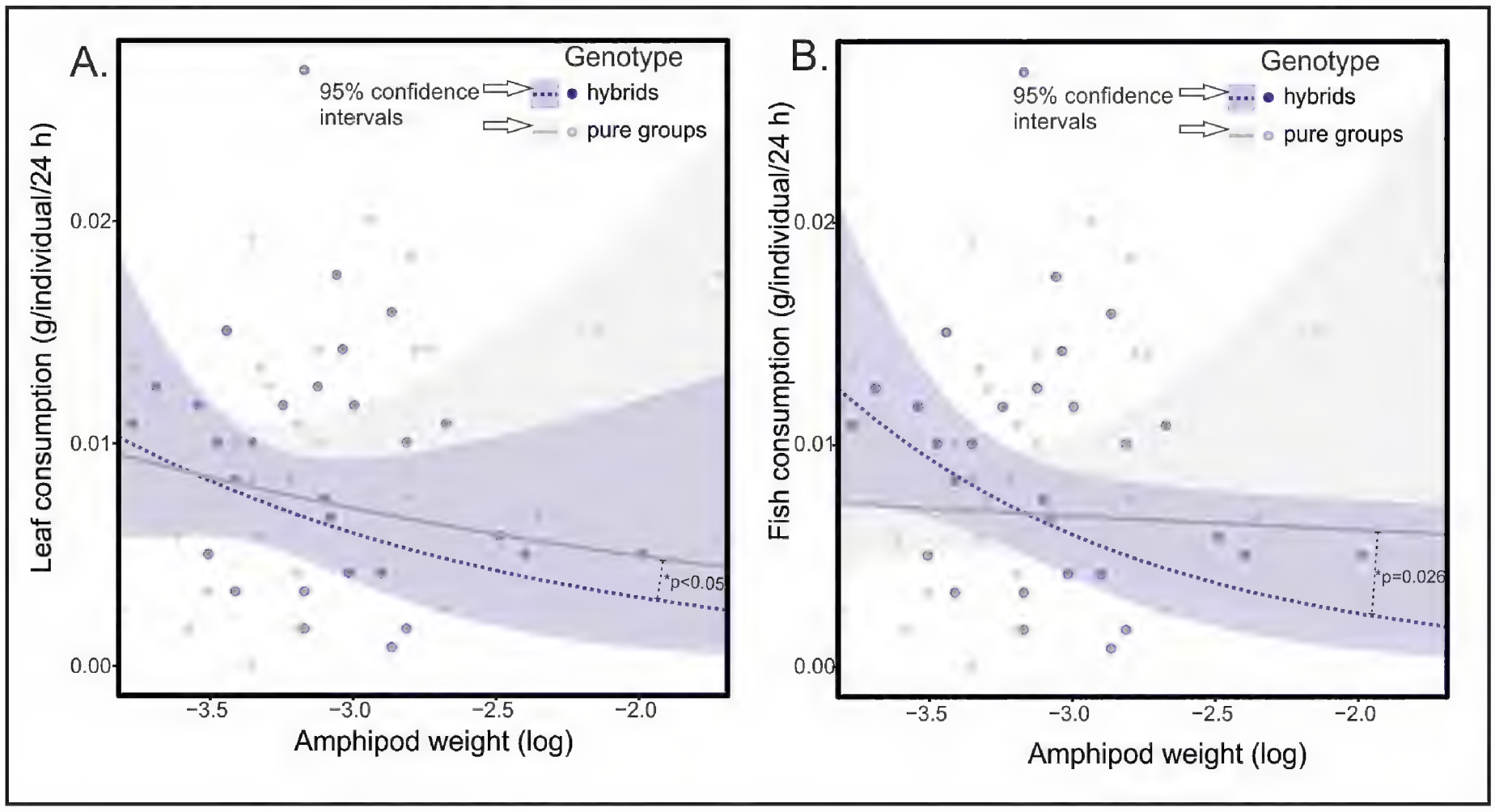

Figure 3. Consumption of leaves in the interaction between genotype and amphipod weight (**A**); consumption of fish in the interaction between genotype and amphipod weight (**B**) predicted by the GLMMs (marginal effects). Statistically significant differences are indicated by asterisks ($p \leq 0.05$; for all pairwise comparisons, see Suppl. material 1: tables S10, S11).

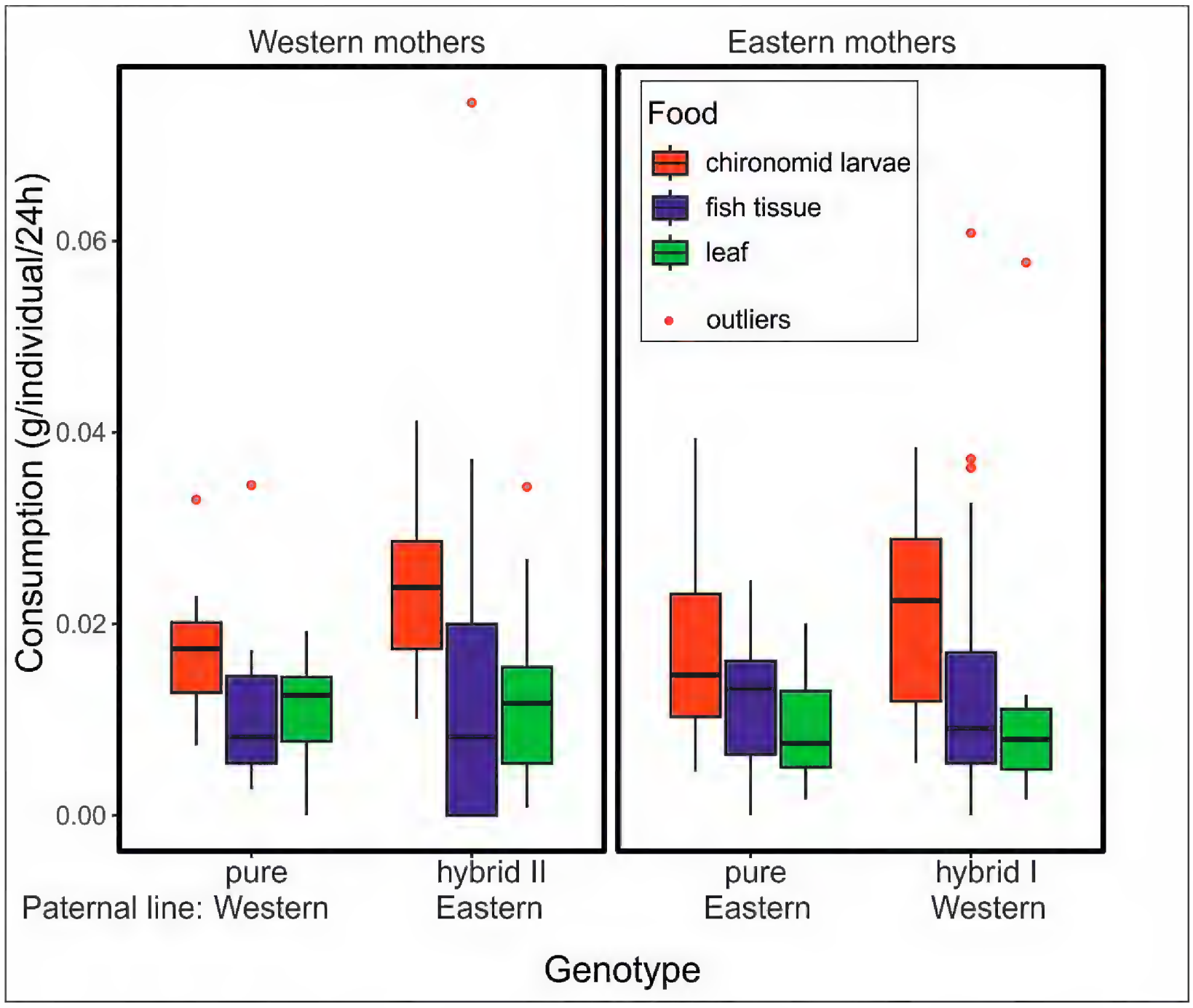

Figure 4. Boxplot for food consumption (g/individual/24 h) of three food items in single-food treatments by origin of maternal line and genotype (hybrid or pure).

Food preference

Leaves (n = 55) were rather avoided – the Ivlev's Selectivity Index value: -0.23 ± 0.51 (Mean ± SD). Selectivity towards this food type was dependent on the sex * amphipod weight interaction (p = 0.02; Table 2, Fig. 5A; for pairwise comparisons, see Suppl. material 1: table S12). Leaf selectivity presented inverted patterns for the sexes according to the weight, being positively correlated for females and negatively for males. Pure genotypes and hybrids of the same paternal origin tended to exhibit similar leaf selectivity (Fig. 6). Fixed effects explained 0.039 (Marginal R^2) of the variance observed.

Amphipods avoided fish consumption (n = 55) – Ivlev's Selectivity Index value: -0.41 ± 0.37 (Mean ± SD) was significantly lower amongst amphipods of Western maternal origin compared to those of the Eastern maternal origin (p = 0.02; Table 2, Fig. 5B), especially amongst amphipods of the pure genotype (significant post-hoc comparison: p < 0.01 in marginally significant origin * genotype interaction: p = 0.08; for pairwise comparisons, see Suppl. material 1: table S13). On the other hand, presence of at least one parent of Western origin contributed to a decrease in fish selectivity amongst their offspring (Fig. 6). Generally, fish selectivity increased with an increase in amphipod weight (p = 0.04; Table 2, Fig. 5C) and was significantly higher amongst larger Eastern maternal origin amphipods of pure genotype than hybrids (post hoc: p = 0.02; for pairwise comparisons, see Suppl. material 1: tables S14, S15). Fixed effects explained 0.034 (Marginal R^2) of the variance observed.

Most of the amphipods exhibited a positive selectivity towards chironomid larvae (n = 55): 0.29 ± 0.33 (Mean ± SD) Ivlev's Selectivity Index value. Selectivity of chironomid larvae exhibited by amphipods of Western origin of maternal line was significantly higher than those of the Eastern origin (p = 0.01; Table 2, Fig. 5F, Fig. 6). Selectivity was significantly dependent on genotype * amphipod weight interaction (p = 0.03; Table 2) with a tendency to grow with an increase of animal body weight in case of hybrids (Fig. 5E; for pairwise comparisons, see Suppl. material 1: table S16). Fixed effects explained 0.020 (Marginal R^2) of the variance observed.

Discussion

This study demonstrates that amphipods exhibit intraspecific differences in food consumption rates and preferences depending on the origin of the parental lines involved in the interbreeding, which allows us to accept hypothesis I. Although the hybrids did not show an increased rate of consumption compared to the pure lines, they did demonstrate higher levels of food specialisation and predation, being partially congruent with hypothesis II. Amphipods showed similar patterns to the parental populations in their food preferences. Those with a Western maternal line origin showed higher levels of predation, while those with an Eastern origin tended to have lower levels of specialisation and a tendency towards omnivory. Specifically, the preference towards chironomid larvae replicated the pattern in the maternal line, allowing hypothesis III to be accepted.

By carrying out experiments on the F1 generation, bred under identical conditions, we were able to study the effect of ancestry on shaping the feeding behaviour of amphipods, while controlling for the effect of the environment. The influence of

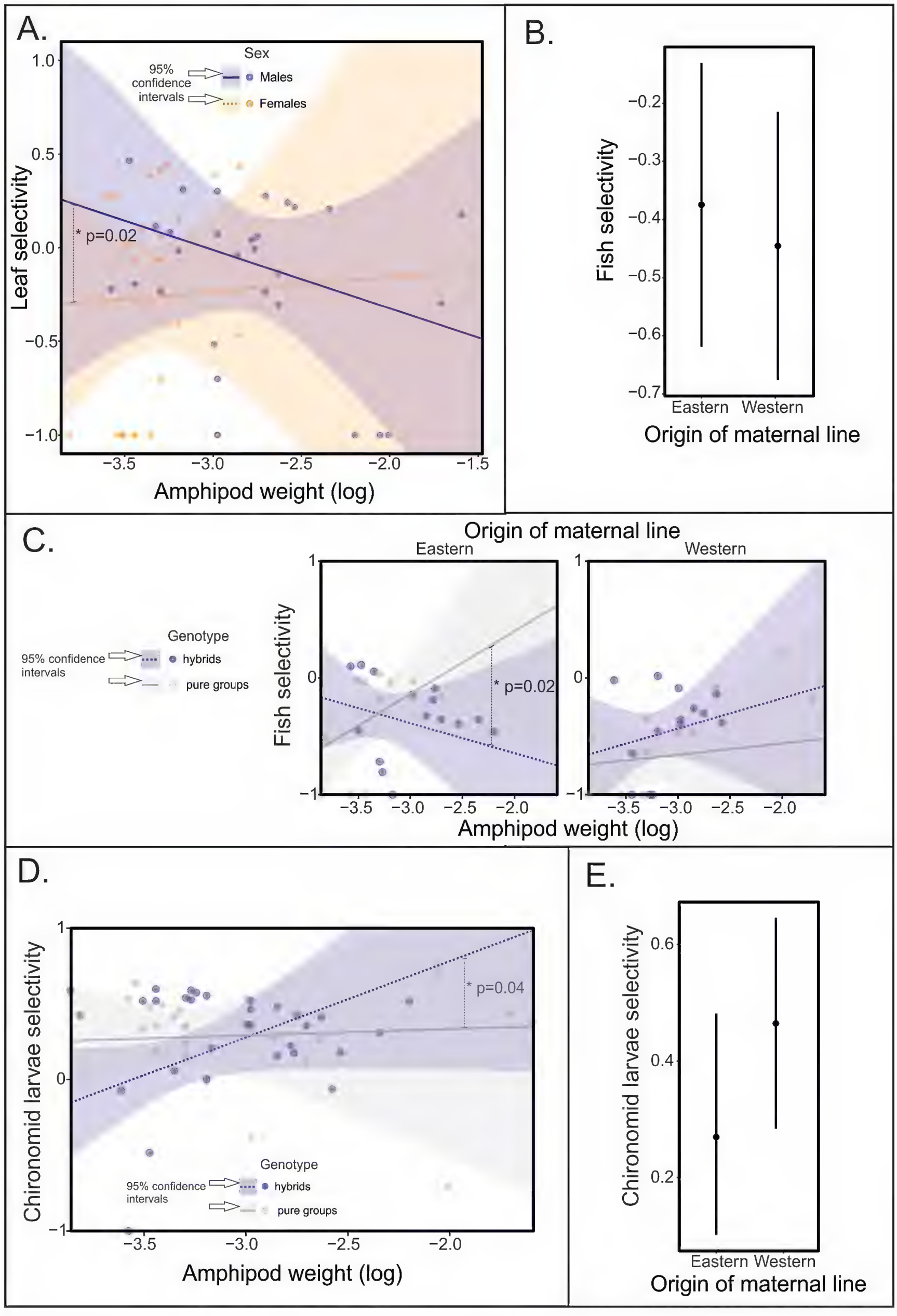

Figure 5. Amphipod food preferences in Experiment II. Selection of leaves depending on the sex * amphipod weight interaction (**A**); selection of fish tissue depending on the origin (**B**) and origin * genotype * amphipod weight interaction (**C**); selection of chironomid larvae depending on the genotype * amphipod weight interaction (**D**) and origin (**E**), predicted by the GLMM (marginal effects). Statistically significant differences are indicated by asterisks ($p \leq 0.05$; for all pairwise comparisons, see Suppl. material 1: tables S12–S16).

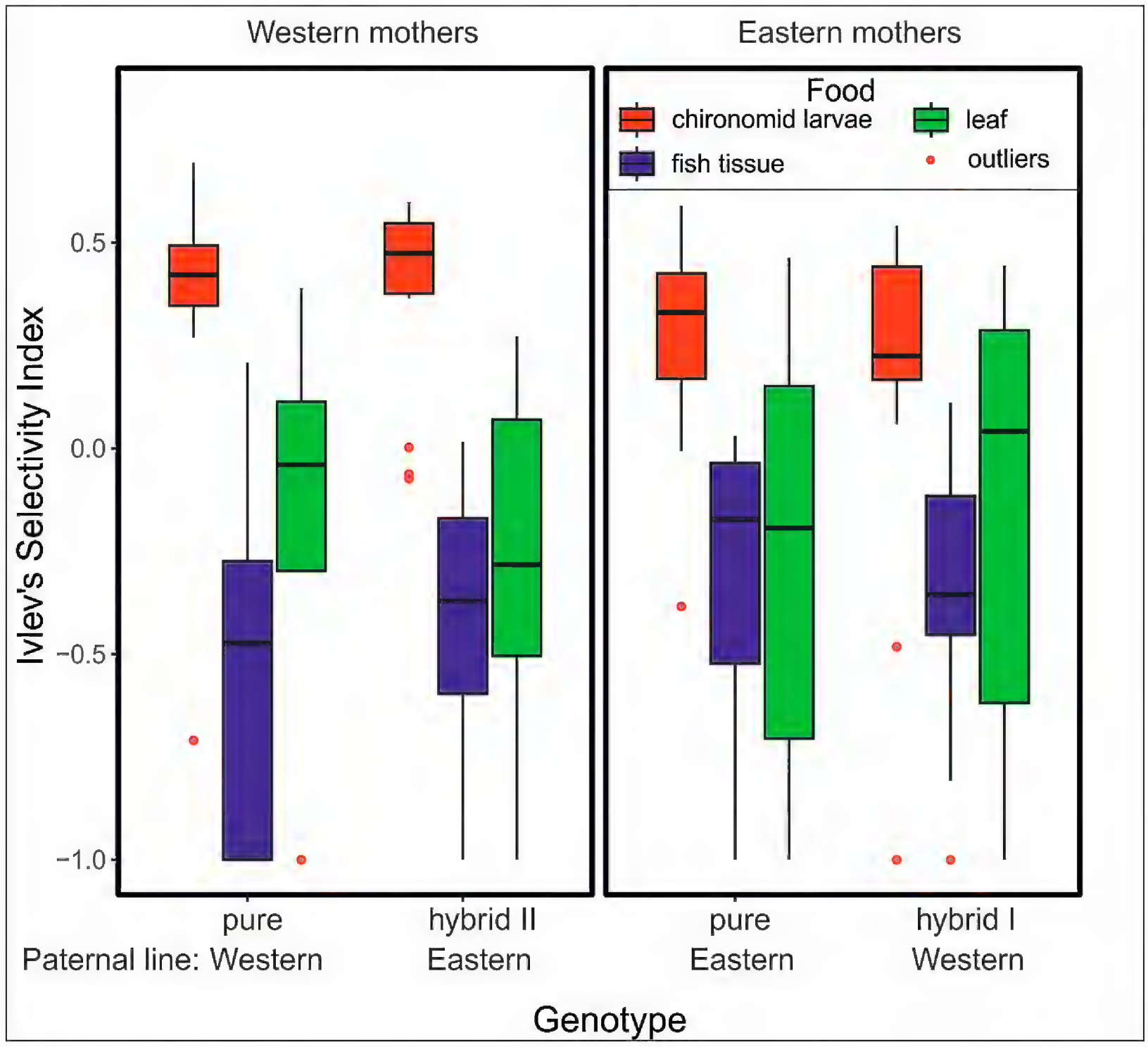

Figure 6. Boxplot for food selectivity index of food preference experiment by origin and genotype.

environmental conditions on shaping invasive traits of local populations are underlined (Oh et al. 2021), while not many of them consider the intraspecific variation amongst populations and thereby genetic background. Our experiments revealed that larger hybrids display decreasing consumption rate of leaves and fish tissue (Fig. 3) probably due to a higher selectivity towards chironomid larvae compared to amphipods of pure origin (Fig. 5E). Overall, we observed that amphipods of the F1 generation display different food preference depending on the origin of their maternal lines, i.e. those of Western origin of maternal line select more chironomid larvae than those of the Eastern origin and the opposite is true for fish tissue selection (Fig. 5B, E). Based on these results, we may conclude that offspring of the Western Group females are more predatory and, therefore, can pose a higher threat to benthic communities than their counterparts of the Eastern origin of their maternal lines. The latter appeared less food-specialised, i.e. consuming not only chironomid larvae, but also plant and dead fish tissues, which would favour their establishment in unstable environments with limited food resources. These observations are congruent with the morphological comparison of feeding-related body traits between both groups (Podwysocki et al. 2025a), as well as with experimental testing food preferences of pure parental populations (Podwysocki et al. 2025c). This means that the choice of fish tissue and live chironomid larvae in the interbreeding F1 generation offspring replicates the patterns typical of the maternal populations.

Inheritance in the maternal line is common in plants (Monty et al. 2009; Alba et al. 2016). Amongst animals, it has been shown amongst others in mammals (Broadhurst 1961), fish (Chivers et al. 2015), invasive ants (Rey et al. 2013) and some other invertebrates. For instance, it was observed that aphids inherit predator avoidance, based on the mother's experience (Keiser and Mondor 2013) and moths inherit expression of immune-related genes (Freitak et al. 2014). There are several possible ways of passing on traits from maternal line to offspring.

The first is the inheritance of mitochondrial DNA (mtDNA), exclusively in the maternal line as the probability of a paternal leakage is very low. Rand (1994) states that thermal conditions and metabolic rate affect the evolution of mtDNA, which is then inherited by offspring. Interestingly, the differences have been noted between Western and Eastern groups of *D. villosus* in terms of temperature preference (Hupało et al. 2018; Podwysocki et al. 2024a) and metabolic rate (Jermacz et al. 2025). This may mean that the different thermal conditions of the environment in which the Western and the Eastern groups occur affect heritable changes in mtDNA (playing a crucial role in cellular metabolism), which, passed from a mother to the offspring, influences different food preferences of the next generations depending on the origin of the parental populations. However, further research on gene flow is required, which was not conducted in these studies. Moreover, what remains unclear in this case is the higher predation rate of the Western Group compared to the Eastern Group, although it is the metabolic rate of the latter that is higher (Jermacz et al. 2025).

Another explanation may be epigenetic inheritance of food preferences. For example, different diets affect heritable differences in gene expression, which is passed on to offspring from mothers in mice (Waterland and Jirtle 2003). It has been shown that caterpillars of *Bicyclus anynana* inherit a preference for food odour from parental diet experience (Gowri and Monteiro 2024). In mangrove crabs, the composition of the gut microbiome was found to be linked to food preference, suggesting a potential mechanism of epigenetic inheritance in the maternal line (Tsang et al. 2024). Amphipods were shown to vary in the composition of the gut microbiome depending on biotic and abiotic factors (Wei et al. 2023). Hence, we may speculate that differences in environmental conditions, including benthic species composition between the Western and Eastern group habitats, may influence differences in microbiome composition, epigenetically inherited by the offspring. On the other hand, the fact that our mesocosm culture ran under identical conditions could decrease such possibility.

In addition, the care of offspring remaining in the marsupia has been demonstrated in amphipods (Tarutis et al. 2005), mainly related to oxygenation and removal of dead eggs (Dick et al. 1998), but less frequent examples of the mother providing food to her offspring were also found (Aoki and Kikuchi 1991; Thiel 1997). We may speculate that the female, by inducing the flow of water in the brood chamber, contributes to the oxygenation of the eggs while supplying the juveniles with organic matter suspension, providing to their offspring the access to varying foods and affecting their learning process. The learning ability and memory, although poorly understood in crustaceans, can be an important factor shaping their feeding behaviour (Shadrin et al. 2024). Although the exact mechanisms of the following of dietary patterns by amphipod offspring are not known, our results clearly indicate the maternal effects in food preferences, which deserve further study.

Interestingly, crossing individuals between the two groups results in some amended traits in the hybrids compared to the offspring of pure lines. We observed that, amongst larger specimens, hybrids exhibit higher selectivity towards chironomid larvae compared to those of pure origin (Fig. 5D) and an opposite tendency observed in case of fish tissue selectivity made by offspring of mothers of Eastern origin (Fig. 5C). Increasing consumption rate with the body weight of consumers is associated with growing energy needs that larger specimens compensate for through dietary changes (van der Velde et al. 2009). Such dietary changes may be quantitative i.e. may include an increase in consumption rate (Woodward et al. 2010; Pellan et al. 2015), which was observed for wild populations of *D. villosus* (Podwysocki et al. 2025c). On the other hand, the increased energy requirements of large individuals can be compensated for by qualitative dietary changes and an increase in selection towards more energetic animal-based foods, especially as larger individuals find it easier to hunt their prey (Parmenter 1980; Iltis et al. 2018). We, therefore, consider that larger hybrids compensate for their enhanced energy costs by refraining from the consumption of low-energy profitable dead fish tissue (Fig. 5C) and by increasing selectivity towards chironomid larvae (Fig. 5D). These findings may suggest a higher metabolic rate of hybrids compared to parental populations which was already observed in some bivalves (Bakhment et al. 2022). Although, in contrast to bivalves, in amphipod hybrids, the higher metabolic rate may be an advantage, for instance, for more effective dispersion. Furthermore, a higher predatory pressure in hybrids may mean that their future meeting in the contact zone will result in producing offspring that are more predatory, posing a greater threat to macroinvertebrate communities compared to pure populations.

The results of our research report that food preferences of amphipods depend on their origin and are subjected to the maternal effect. Hybrids may achieve higher invasive potential due to higher diet specialisation (Fig. 7). Consequently, they may pose a higher threat to macroinvertebrates. However, it is worth noting some limitations of our research. Although our simulation shows that hybrid offspring display similar food preferences as their maternal populations and may have a higher invasive potential than paternal populations, this trend may be reduced in natural conditions over the long term. Despite the vigour of the first generation of hybrids (heterosis), their progeny segregate and traits can mix and reduce the effect of heterosis in subsequent generations (Huang et al. 2016). Hybrids can benefit from heterosis through enhanced growth rate, fecundity and overall fitness and maintaining their vigour in the next generation is possible, but depends on favourable conditions and population structure (Wakchaure et al. 2015). To better understand this process and its potential consequences, we propose that future research on this problem should focus on the following aspects:

1) The advantage of interbreeding over inbreeding will be possible, amongst other things, if preference towards partners from different groups are higher. Therefore, we propose it be experimentally tested whether amphipod pairing in praecopulae is a random process or the result of a preference towards a partner from the same or a different population. Testing how males from both groups compete for access to a female and whether female preferences depend on male origin would allow us to address these doubts and clarify the potential advantage of interbreeding over inbreeding.

2) Since the interbreeding scenario of these groups has not yet been realised in nature, long-term observations should be carried out under mesocosm breeding conditions to obtain the next generations and test whether the vigour of the hybrids persists or declines in the next generations and how this affects their fitness.
3) Heterosis can include a myriad of traits favouring the invasive potential of hybrids. For instance, amphibian hybrids have been found to move faster (Johnson et al. 2010). Although we tested food preference, other aspects of their biology, potentially important for invasion success, should also be tested in the future, amongst them being reproduction, dispersal and predator avoidance. Such studies will provide a complete picture of the biology of the inter-population hybrids of invasive species and enable more effective predictions of the further course of the invasion and potential effects on native fauna and environmental functioning.

This research provided insights into how the food preferences of individual populations are influenced by their origin interpopulation admixture and how their interbreeding may affect the invasive potential of their offspring. The novelty of our approach is testing the influence of the genetic component on the food preferences of amphipods when environmental conditions are controlled and exploring the possible inheritance patterns of these preferences. As feeding habits are one of the most important traits shaping invasiveness, the results of such studies are crucial for better predicting further expansion pathways of invasive species and their impact on native biota.

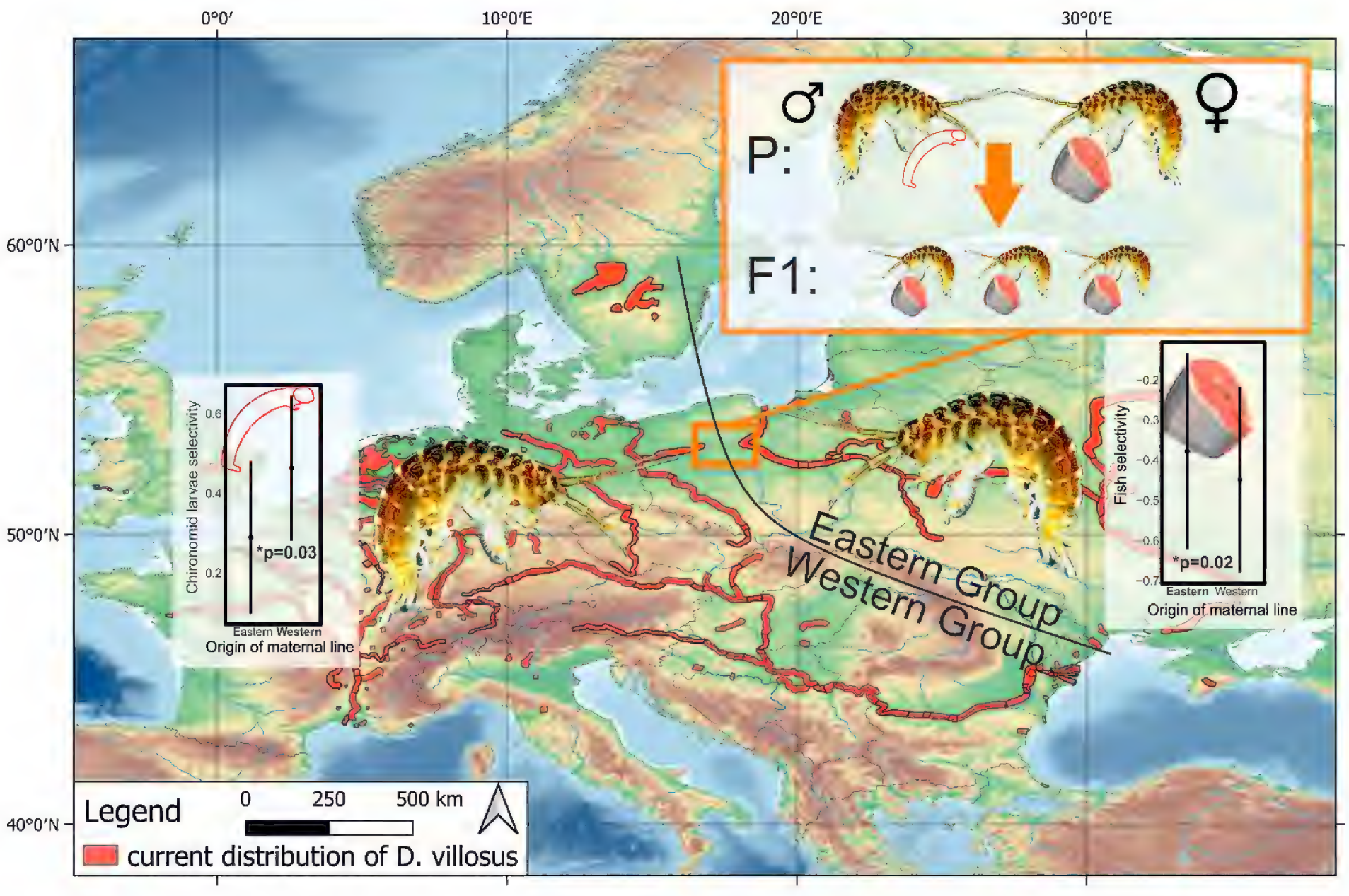

Figure 7. Summary of the main findings of the study.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualisation: KP, JK, ESM, ŁJ, AD, TR, KBS; Data curation: KP, ESM; Formal analysis: KP; Funding acquisition: TR; Investigation: KP; Methodology: KP, JK, ESM, ŁJ, AD, TR, KBS; Project administration: KP, TR; Resources: KP, ESM, JK, ŁJ, AD, TR, KBS; Supervision: TR, KBS; Validation: JK; Visualisation: KP; Writing – original draft: KP; Writing – review and editing: KP, ESM, JK, ŁJ, TR, KBS, AD.

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Data availability

Data are available in the supplementary materials.

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Supplementary material 1

Parameters, results and model selections

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